INFLUENCE OF TEMPERATURE AND LARVAL DENSITY ON FLIGHT PERFORMANCE OF *DIABROTICA VIRGIFERA VIRGIFERA* LECONTE (COLEOPTERA: CHRYSOMELIDAE)

STEVEN E. NARANJO[1]

USDA-ARS, Northern Grain Insects Research Laboratory, RR #3, Brookings, South Dakota, USA 57006

Abstract

Can. Ent. 123: 187–196 (1991)

The influence of temperature and larval density on the flight performance of *Diabrotica virgifera virgifera* LeConte was quantified in the laboratory using a tethered flight system. Temperature had a significant influence on trivial flight performance in males and in both young (5 day) and older (25 day) females. The proportion of beetles undertaking trivial flight, and trivial flight duration and frequency peaked at temperatures around 20–25°C. Generally, males were more active than females at lower temperatures. Female beetles did not display sustained flight behavior at 15 or 35°C and males did not undertake sustained flight at 30 or 35°C. Sustained flight duration was unaffected by temperature. Rearing larvae at different densities influenced adult size but had only subtle effects on adult flight performance. Larval density significantly influenced trivial flight duration and frequency of older females and flight frequency of males but had no effect on young females. In general, trivial flight performance peaked when larvae were reared at moderate densities (500–750 per primary rearing container). In young females the propensity for sustained flight, but not flight duration, declined with increasing larval density.

Naranjo, S.E. 1991. L'influence de la température et de la densité larvaire sur l'exécution de vol chez *Diabrotica virgifera virgifera* LeConte (Coleoptera: Chrysomelidae). *Can. Ent.* 123: 187–196.

Résumé

L'influence de la température et de la densité larvaire sur l'exécution de vol des adultes de *Diabrotica virgifera virgifera* LeConte a été évaluée quantitativement en utilisant un système attaché du vol. La température a eu une influence importante sur l'exécution du vol banal pour les mâles, et pour les femelles âgées de 5 jours et celles âgées de 25 jours, toutes les deux. La proportion d'adultes qui a entrepris le vol banal, et la durée et fréquence de ce vol ont atteint les maximums aux températures autour 20–25°C. Généralement, les mâles ont été plus actifs que les femelles aux basses températures. Les adultes du sexe féminin n'ont pas présenté le vol soutenu à 15 ou à 35°C et les mâles n'ont pas entrepris le vol soutenu à 30 ou à 35°C. La durée du vol soutenu n'a pas été touchée par la température. L'élevage des larves à des densités différentes a eu une influence sur la grosseur des adultes, mais n'a eu que des effets subtiles sur l'exécution du vol par ceux-ci. La densité larvaire a eu une influence importante en ce qui concerne la durée du vol banal et la fréquence de vol des femelles âgées, et la fréquence du vol de mâles, mais a été sans effet en ce qui concerne les jeunes femelles. Par l'habitude, l'exécution du vol banal a atteint son maximum quand les larves avaient été élevées dans une densité modérée (500–750 par bac d'élevage primaire). Dans le cas de jeunes femelles, la tendance naturelle du vol soutenu a diminué en mesure que la densité larvaire a augmenté, ce qui n'a pas été le cas pour la durée du vol.

Introduction

Corn rootworms, *Diabrotica* spp., are ubiquitous throughout the major corn growing regions of the United States and Canada and are considered serious pests in continuous corn production systems. The insects are univoltine (but see Krysan et al. 1986), overwinter as eggs, and, as larvae, are functionally monophagous on corn and relatively immobile. Thus, the continued presence of corn rootworm populations in a particular site from

[1]Present address: Western Cotton Research Laboratory, USDA-ARS, 4135 E. Broadway Road, Phoenix, Arizona, USA 85040.

year to year and their colonization of new cornfields depends on the dispersive and ovipositional behaviors of adult beetles. Some progress has been made toward understanding how dispersal influences corn rootworm population dynamics (Cinereski and Chiang 1968; Hill and Mayo 1980; Godfrey and Turpin 1983; Haddock 1984; Coats et al. 1986; Grant and Seevers 1989; Naranjo and Sawyer 1989), yet we still require considerable knowledge to develop realistic models of beetle movement and population dynamics to aid the development of management strategies.

In particular, little is known of the impact of certain environmental and biological factors on beetle movement. Coats et al. (1986) showed that flight behavior of female *Diabrotica virgifera virgifera* LeConte, the western corn rootworm, was influenced by age and reproductive status and Naranjo (1990) found differences in flight behavior of male and female western corn rootworms. VanWoerkom et al. (1980) reported that adult western corn rootworm activity was strongly influenced by constant and fluctuating temperatures; however, they did not relate temperature to individual components of flight performance. There is also evidence from field and greenhouse studies that population density influences various aspects of the biology of western corn rootworms. Increased larval density has been shown to lengthen larval development times, and reduce adult survival, fecundity, and size (Branson and Sutter 1985; Weiss et al. 1985; Elliott et al. 1989). This study was conducted to examine and quantify the impact of temperature and larval population density on individual components of the flight behavior of *D. virgifera virgifera*. An automated flight system was used to measure flight performance of male and female beetles under controlled conditions.

Materials and Methods

Flight Performance Assays. Flight assays were performed on a computer-monitored flight-device described by Wales et al. (1985) and Barfield et al. (1988) and modified by Naranjo (1990) for testing corn rootworm beetles. Beetles were anesthetized with CO_2 (exposure time <1 min) and tethered by the pronotum to the end of the flight arm with dental wax. Beetles were flown for 23 h beginning 1000–1200 hours CST. For each beetle the device recorded the clock time of the initiation and termination of each individual flight, and the number of flights over the 23-h assay period. During flight evaluations, beetles were not fed and remained suspended above the substrate. Beetles that died before completing the 23-h assay were excluded from analyses.

The flight system comprised 24 actographs which were housed in two walk-in environmental chambers that could be maintained at chosen constant temperatures. All assays described below were conducted at $60 \pm 10\%$ RH with a 14L:10D photoperiod.

Temperature Studies. Western corn rootworm beetles were obtained from a colony maintained at the Northern Grain Insects Research Laboratory. The insects had been in culture approximately two to three generations. Flight assays were conducted at constant temperatures of 15, 20, 25, 30, and 35°C (all ± 0.5°C). Beetles were tethered and allowed to acclimate to experimental temperatures for about 1 h prior to recording flight behavior. Three experimental groups were tested at each temperature: 5- to 7-day-old mated females, 23- to 25-day-old mated females, and 10- to 15-day-old males. These age groups were selected to contrast the behavior of pre-ovipositional and gravid female beetles. Flight activity peaks in females 5–6 days of age (Coats et al. 1986). Male flight behavior changes little with age (Naranjo 1990) and so only one age group was selected for assay. A total of 48 beetles were tested for each experimental group and temperature.

Larval Density Studies. Using established laboratory rearing protocols (Branson et al. 1988), adult western corn rootworms were produced from larvae that were reared at different densities. Preliminary rearing trials indicated that adult size (measured by head-capsule width) could be manipulated by changing the number of western corn rootworm eggs placed in primary rearing containers (6.3 by 15.3 cm diameter). Larvae were reared at densities of 250, 500, 750, and 1200 eggs per primary container. By comparison, standard colony rearing utilizes 500–600 eggs per primary container and produces adults representative of unstressed adults in the field (Branson and Sutter 1985; Branson et al. 1988). Three experimental groups were tested at each density: 5- to 7-day-old mated females, 23- to 25-day-old mated females, and 10- to 15-day-old males. A total of 45–50 beetles were tested for each group and density, and assays were conducted at 25±0.5°C.

Statistical Analysis. For statistical analyses the data on flight performance of each beetle were summarized as follows: First, individual flights were categorized as either trivial (<20 min in duration) or sustained (≥20 min in duration) (see Naranjo 1990 for discussion of this distinction). Second, durations of individual trivial or sustained flights were averaged for each beetle and these means, along with number of flights of each type per beetle in the 23-h assay period, were the flight parameters analyzed. Differences between treatments were analyzed separately for each sex/age group with nonparametric analysis of variance [Kruskal-Wallis tests (Conover 1980)]. Regression analysis was performed to test for and quantify relationships between temperature or larval density and beetle flight performance. Because flight parameter distributions were highly right-skewed, data were log-transformed prior to regression analysis, but results are presented in a back-transformed state. Finally, *G*-tests (Sokal and Rohlf 1981) were used to compare proportions of beetles flying between treatments within studies. Due to small sample sizes and low cell frequencies, Fisher's exact tests (Zar 1984) were used to examine treatment effects on the proportion of beetles undertaking sustained flight.

Results and Discussion

Temperature. Temperature is considered one of the more significant features of weather that influences the dispersal and migration of insects (Taylor 1963; Johnson 1969; McManus 1988). Results here suggest that temperature may have a significant effect on dispersal of *D. v. virgifera* through its effect on some of the individual components of flight performance, including propensity for flight and the duration and frequency of individual flights.

The propensity for trivial flight, measured as the proportion of beetles undertaking at least one trivial flight, was significantly influenced by temperature in all test groups ($P<0.05$, *G*-tests) (Table 1). Males, and 5- and 25-day-old females all responded similarly to temperature. The proportion flying was lowest at 15°C, increased with temperature up to 25°C, and then declined again as temperature approached 35°C.

Temperature had a significant influence on both trivial flight duration and frequency of flight for all three groups ($P<0.01$, Kruskal-Wallis). Preliminary plots of flight performance parameters against temperature indicated that relationships were curvilinear. Therefore quadratic regressions were performed on log-transformed data to establish the strength of these relationships and to provide quantitative descriptions of temperature on western corn rootworm flight performance. Regressions were significant ($P<0.01$) in all instances and provided good fits to the data (Fig. 1). Regression equations for average trivial flight duration are given by:

5-day-old females: $x = \exp(0.5495T - 0.0116T^2 - 7.2309)$
25-day-old females: $x = \exp(0.5187T - 0.0103T^2 - 7.8140)$
15-day-old males: $x = \exp(0.1772T - 0.0048T^2 - 2.3236)$

where T is temperature in °C. Regressions for the mean frequency of trivial flight within the 23-h assay period are given by:

5-day-old females: $x = \exp(0.8811T - 0.0184T^2 - 6.4406)$
25-day-old females: $x = \exp(0.6538T - 0.0127T^2 - 4.6916)$
15-day-old males: $x = \exp(0.4697T - 0.0095T^2 - 2.2789)$

Table 1. Proportion of western corn rootworm adults undertaking trivial flight (flights <20 min) in relation to temperature and larval density

	5-day-old female			25-day-old female			15-day-old male		
Factor	No. tested	No. flying	Proportion flying	No. tested	No. flying	Proportion flying	No. tested	No. flying	Proportion flying
Temperature (°C)									
15	46	16	46	16	0.348	46	16	0.348	
		nt 0.348							
20	46	37	0.804	45	37	0.822	44	37	0.841
25	46	42	0.913	46	40	0.870	46	45	0.978
30	45	37	0.822	45	34	0.756	46	40	0.870
35	46	26	0.565	45	22	0.489	45	30	0.667
G *			9.54*			9.56*			10.27*
Larval density†									
250	50	46	0.920	46	44	0.957	46	38	0.826
500	42	40	0.952	46	46	1.000	44	28	0.636
750	40	36	0.900	46	34	0.739	42	40	0.952
1200	46	36	0.783	46	32	0.696	44	40	0.909
G			0.45NS			2.05NS			1.77NS

**G*-test for independence; $P<0.05$. NS = not significant.
†Number of western corn rootworm eggs per primary rearing container.

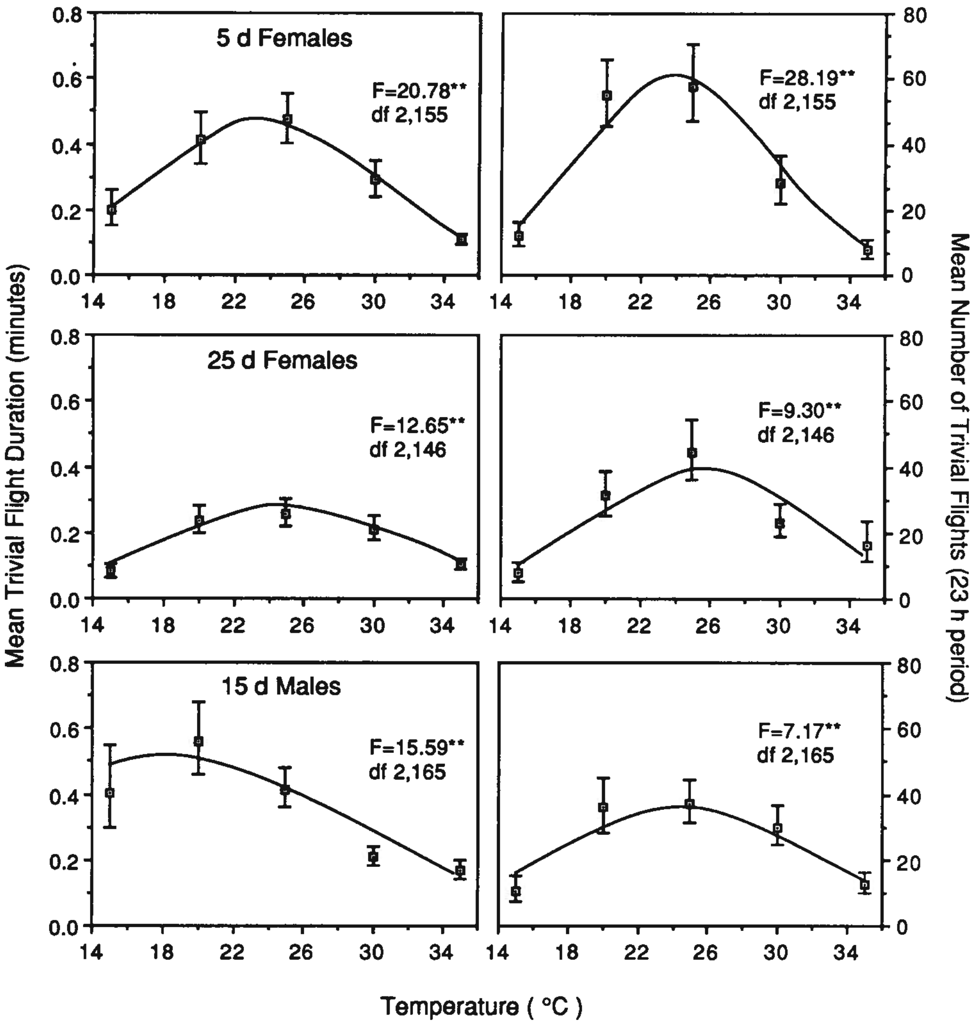

FIG. 1. Relationships between trivial flight performance parameters and temperature for 5- and 25-day-old female and 15-day-old male western corn rootworm adults. Quadratic regressions were performed using log-transformed data from each individual beetle, but, for clarity, only back-transformed means with standard error bars from each temperature are presented. *F* statistics and degrees of freedom are given for regressions (**$P<0.01$).

Trivial flight activity in females peaked at temperatures near 25°C, and activity levels were generally lower in 25-day-old than in 5-day-old females. In comparison with females, males were more active at lower temperatures with a peak in trivial flight activity around 20°C. Also, in comparison with females, males displayed much greater flight durations at 15°C. In both sexes, durations and frequencies of trivial flight were significantly curtailed at temperatures approaching 35°C.

In comparison with trivial flight, the influence of temperature on sustained flight performance of western corn rootworms was more subtle, and, due to the relative rarity of sustained flight, more difficult to analyze. Five-day-old females did not undertake sustained flight at either 15 or 35°C, and there were no significant differences in the propensity for sustained flight ($P>0.05$; Fisher's exact test) or the mean duration of sustained flight

Table 2. Influence of temperature and larval population density on sustained flight (flights ≥ 20 min) behavior of western corn rootworm adults

Factor	5-day-old females			25-day-old females			15-day-old males		
	Proportion flying*	Median duration (min)	*N*	Proportion flying*	Median duration (min)	*N*	Proportion flying*	Median duration (min)	*N*
Temperature (°C)									
15	0 a	—	0	0 a	—	0	0.022a	26.45	1
20	0.152b	35.43	7	0 a	—	0	0.136a	25.34	6
25	0.065ab	24.35	3	0.065a	32.08	3	0.065a	25.45	3
30	0.044ab	40.39	2	0 a	—	0	0 a	—	0
35	0 a	—	0	0 a	—	0	0 a	—	0
Larval density†									
250	0.200a	32.45	10	0.044a	36.00	2	0 a	—	0
500	0.174a	35.57	8	0 a	—	0	0.046a	24.85	2
750	0.05b	33.61	2	0.044a	33.95	2	0.048a	22.13	2
1200	0.087ab	24.64	4	0 a	—	0	0.046a	20.40	2

*Proportions followed by the same letter are not significantly different ($P>0.05$) by pairwise comparisons with Fisher's exact test.
†Number of western corn rootworm eggs per primary rearing container.

at temperatures between 20 and 30°C ($P>0.05$; Kruskal-Wallis) (Table 2). The incidence of sustained flight was generally lower in the two remaining test groups. Sustained flight was observed in 25-day-old females only at 25°C and then in only 6.5% of those tested. Males undertook sustained flight only at temperatures between 15 and 25°C and generally took flights of shorter duration in comparison with females. Patterns of sustained flight reinforced those of trivial flight in that males displayed greater flight activity at lower temperatures.

These findings are in general agreement with studies that used other indices of insect activity. Utilizing a motion-detecting system in the laboratory, VanWoerkom et al. (1980) found that adult western corn rootworm activity was highly temperature-dependent with peaks of activity around 25°C for both sexes. They found that activity was negligible at temperatures of 10 or 40°C and that, in comparison with females, males were more active at 20°C and less active at 35°C. Witkowski et al. (1975), using sticky traps, reported that peak flight activity of western corn rootworms in the field coincided with temperatures between 22 and 27°C.

Typically, there are threshold temperatures below which insects are unable to take off and fly (McManus 1988). Western corn rootworm beetles displayed some flight activity at the lowest temperature tested (15°C); however, in preliminary tests with a limited number of beetles no flight was observed at 10°C (unpublished data). Thus, the threshold for flight is probably somewhere between 10 and 15°C for both sexes, and most likely lower for males. The sharp drop in flight activity at temperatures above 25°C suggests that there is also a high temperature threshold (above 35°C) above which beetles will not or are unable to fly. The slightly different response of beetles to temperature in relation to long-duration flight suggests a difference in thresholds for take off and the ability to maintain flight. For example, females undertook trivial flights at all temperatures but sustained flight only at temperatures between 20 and 30°C. Thus, although take off was possible at 15 and 35°C, beetles were apparently unable to maintain flights longer than 20 min at these temperatures. Further work at a greater range of temperatures will be necessary to define accurately these various temperature thresholds for flight of western corn rootworm beetles.

Larval Density. Larvae reared at densities of 500, 750, and 1200 per primary container produced adult females similar to adults from fields artificially infested with western corn rootworm eggs (collected from adults the previous fall) at levels of 300, 600, and 1200–2400 eggs per 30.5 cm of row, respectively (Branson and Sutter 1985). Head-capsule widths [the standard measurement for judging western corn rootworm adult quality and size (Branson et al. 1988)] were ($\bar{x} \pm$ SE, $N>50$): 250 per container, female 1.28 ± 0.006 mm, male 1.26 ± 0.007 mm; 500 per container, female 1.24 ± 0.016 mm, male 1.25 ± 0.012 mm; 750 per container, female 1.21 ± 0.016 mm, male 1.22 ± 0.008 mm; and 1200 per container, female 1.16 ± 0.015 mm, male 1.20 ± 0.009 mm. Thus, based on adult size, beetles reared here appear representative of those produced under various levels of larval crowding in the field.

In comparison with temperature, larval population density had a lesser and somewhat inconsistent effect on western corn rootworm flight performance. The proportion of beetles undertaking trivial flight generally declined with increasing larval density, at least for females; however, these proportions did not differ significantly from one another within a given age or sex group ($P>0.05$, G-tests) (Table 1). Larval density had a significant effect on trivial flight duration and frequency of flight in 25-day-old females ($P<0.05$, Kruskal-Wallis) but not on either flight performance parameter in 5-day-old females or males ($P>0.05$). Relationships between flight performance and larval density were curvilinear (Fig. 2). Regression analysis indicated significant quadratic relationships between larval density and both trivial flight duration and frequency of flight for 25-day-old females

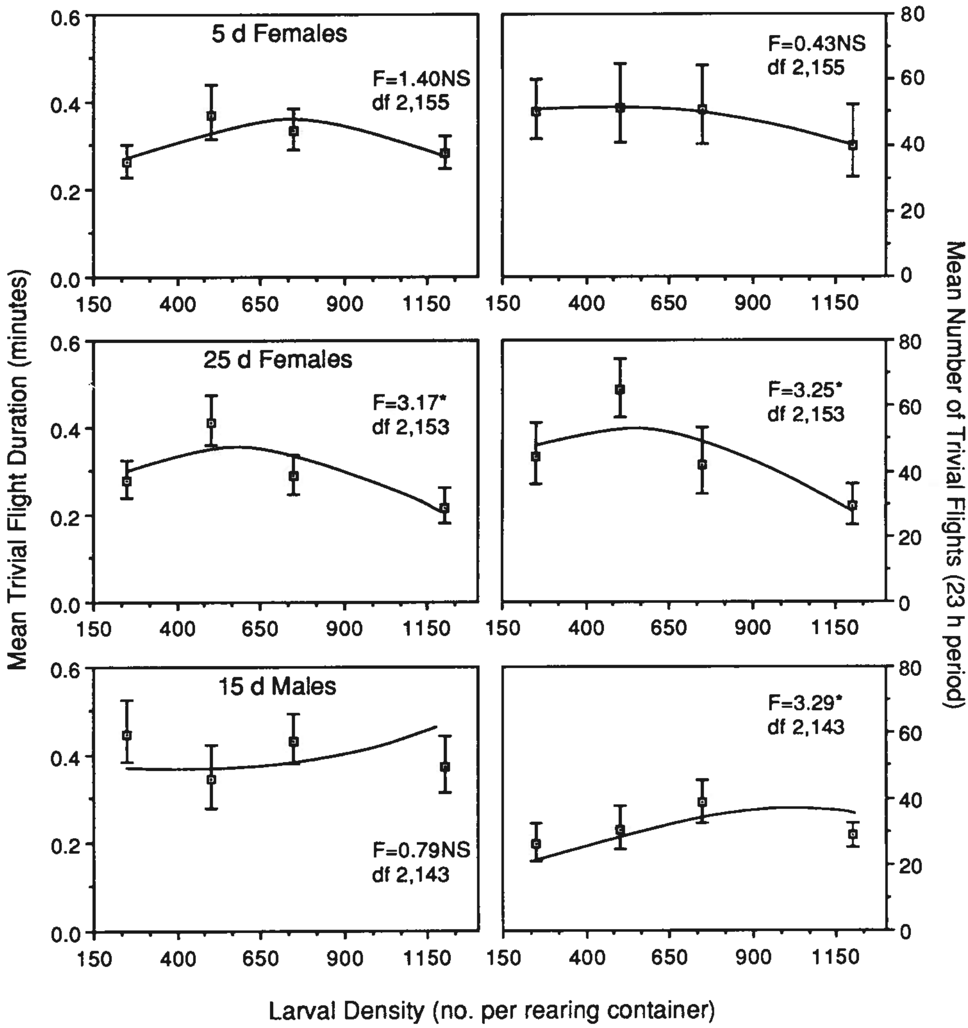

FIG. 2. Relationships between trivial flight performance parameters and larval density (no. per larval rearing container) for 5- and 25-day-old female and 15-day-old male western corn rootworm adults. Quadratic regressions were performed using log-transformed data from each individual beetle, but, for clarity, only back-transformed means with standard error bars from each temperature are presented. *F* statistics and degrees of freedom are given for regressions (**P*<0.05).

and frequency of flight for male western corn rootworm. The regression equation for mean trivial flight duration in 25-day-old females is:

$$x = \exp(0.0017D - 0.0000014D^2 - 1.5554)$$

and equations for mean frequency of flight in 25-day-old females and 15-day-old males are, respectively:

$$x = \exp(0.0015D - 0.0000014D^2 + 3.5806)$$
$$x = \exp(0.0020D - 0.0000009D^2 + 2.4693)$$

where *D* is larval density. For 25-day-old females, mean flight durations and frequencies peaked when beetles were reared at 500 larvae per container. The mean frequency of flight in males peaked in beetles reared at 750 larvae per container.

Some 5-day-old females undertook sustained flight regardless of the density at which they were reared as larvae. However, the proportion of individuals demonstrating such flight generally declined with increasing larval density (Table 2). The duration of sustained flight in 5-day-old females was not significantly influenced by larval density ($P>0.05$; Kruskal-Wallis). The incidence of sustained flight was lower in 25-day-old females and males, and there were no discernible nor significant patterns in relation to larval density (Table 2).

Population density influences many aspects of insect biology and population ecology (Peters and Barbosa 1977). Several authors have reported on the effects of population density on corn rootworms. Weiss et al. (1985) demonstrated that increasing densities of western corn rootworm larvae in potted corn in the greenhouse resulted in delays in larval development, male-skewed sex ratios in emerging adults, and reduced adult size and survival. Similar effects due to crowding have been shown in the field. By varying the rate of artificial infestation in field plots, Branson and Sutter (1985) found that rates of infestation over 300 eggs per 30.5 cm of row reduced adult size, and rates over 600 reduced adult longevity and fecundity. Elliott et al. (1989) further verified these results by showing reductions in immature survival and development rates at densities over 1200 eggs per 30.5 cm of row.

Thus, the effects of larval crowding have the potential to influence significantly the population dynamics of western corn rootworm directly through changes in development and survival and in adult quality. There are numerous examples among insects in which features of adult behavior, including flight behavior, are influenced by crowding (Peters and Barbosa 1977). For example, crowding influences the production of alate aphids (Shaw 1970*a*) and may also affect the tendency for migratory behavior (Shaw 1970*b*). Also, in some insects, larval crowding has been shown to influence various aspects of the flight behavior of resultant adults (e.g. Hirata 1956; Nayar and Sauerman 1969).

The curvilinear response of trivial flight performance to larval population density here, though not always statistically significant, suggests a dual effect of density over the range of values examined. The positive relationship between flight activity and larval density up to a moderate level suggests increased flight activity in response to crowding. However, the subsequent decline in flight activity from moderate to high densities suggests physiological stress induced by severe crowding. In contrast, sustained flight generally declined with increasing larval density suggesting that crowding caused stress that reduced the physiological capacity of the adult to undertake long duration flight.

It is difficult to extrapolate the results of these studies to behavior of beetles in the field; however, findings do indicate that both temperature and, to a lesser degree, larval population density may influence the rate and extent of dispersal of western corn rootworms in the field. Temperature will vary considerably over the season and over the course of the day, and it may be necessary to consider its effect in models predicting corn rootworm movement. The influence of population density is more problematic because it is difficult to relate densities in rearing containers to those in the field. Based on adult size the highest density in this study was roughly equivalent to between 1200 and 2400 eggs per 30.5 cm of row. Branson and Sutter (1985) and Elliott et al. (1989) suggest these high densities may not be representative of natural infestations. If so, results here suggest we might expect to see a subtle increase in dispersal activity (at least through trivial flight) with increasing larval density. Further work, including the consideration of adult density, will be needed to clarify the role of population density in corn rootworm dispersal.

References

Barfield, C.S., D.J. Waters, and H.W. Beck. 1988. Flight device and database management system for quantifying insect flight and oviposition. *J. econ. Ent.* **81**: 1506–1509.

Branson, T.F., J.J. Jackson, and G.R. Sutter. 1988. Improved method for rearing *Diabrotica virgifera virgifera* (Coleoptera: Chrysomelidae). *J. econ. Ent.* **81**: 410–414.

Branson, T.F., and G.R. Sutter. 1985. Influence of population density of immature on size, longevity, and fecundity of adult *Diabrotica virgifera virgifera* (Coleoptera: Chrysomelidae). *Environ. Ent.* **14**: 687–690.

Cinereski, J.E., and H.C. Chiang. 1968. The pattern of movement of adults of the northern corn rootworm inside and outside of corn fields. *J. econ. Ent.* **61**: 1531–1536.

Coats, S.A., J.J. Tollefson, and J.A. Mutchmor. 1986. Study of migratory flight in the western corn rootworm (Coleoptera: Chrysomelidae). *Environ. Ent.* **15**: 620–625.

Conover, W.J. 1980. Practical Nonparametric Statistics, 2nd ed. John Wiley and Sons, New York, NY. 493 pp.

Elliott, N.C., G.R. Sutter, T.F. Branson, and J.R. Fisher. 1989. Effect of population density of immatures on survival and development of the western corn rootworm (Coleoptera: Chrysomelidae). *J. ent. Sci.* **24**: 209–213.

Godfrey, L.D., and F.T. Turpin. 1983. Comparison of western corn rootworm (Coleoptera: Chrysomelidae) adult populations and economic thresholds in first-year and continuous corn fields. *J. econ. Ent.* **76**: 1028–1032.

Grant, R.H., and K.P. Seevers. 1989. Local and long-range movement of adult western corn rootworm (Coleoptera: Chrysomelidae) as evidenced by washup along southern Lake Michigan shores. *Environ. Ent.* **18**: 266–272.

Haddock, R.C. 1984. Orientation and movement of the northern corn rootworm, *Diabrotica barberi* (Coleoptera: Chrysomelidae) over large and small distances. Ph.D. dissertation, Cornell University, Ithaca, NY.

Hill, R.E., and ZB Mayo. 1980. Distribution and abundance of corn rootworm species as influenced by topography and crop rotation in eastern Nebraska. *Environ. Ent.* **9**: 122–127.

Hirata, S. 1956. Influence of larval density upon variations observed in the adult stage on the phase variation of cabbage armyworm, *Mamestra brassicae*. II. Influence of larval density on the variations observed in the adult. *Res. Pop. Ecol.* **3**: 79–92.

Johnson, C.G. 1969. Migration and Dispersal of Insects by Flight. Methuen, London. 763 pp.

Krysan, J.L., D.E. Foster, T.F. Branson, K.R. Ostlie, and W.S. Cranshaw. 1986. Two years before hatch: Rootworms adapt to crop rotation. *Bull. ent. Soc. Am.* **32**: 250–253.

McManus, M.L. 1988. Weather, behavior and insect dispersal. pp. 71–94 *in* Sahota, T.S., and C.S. Holling (Eds.), Paths from a Viewpoint: The Wellington Festschrift on Insect Ecology. *Mem. ent. Soc. Can.* 146. 213 pp.

Naranjo, S.E. 1990. Comparative flight behavior of *Diabrotica virgifera virgifera* and *Diabrotica barberi* in the laboratory. *Entomologia exp. appl.* **55**: 79–90.

Naranjo, S.E., and A.J. Sawyer. 1989. A simulation model of northern corn rootworm, *Diabrotica barberi* (Coleoptera: Chrysomelidae), population dynamics and oviposition: Significance of host plant phenology. *Can. Ent.* **121**: 169–191.

Nayar, J.K., and D.M. Sauerman, Jr. 1969. Flight behavior and phase polymorphism in the mosquito *Aedes taeniorhynchus*. *Entomologia exp. appl.* **12**: 365–375.

Peters, T.M., and P. Barbosa. 1977. Influence of population density on size, fecundity and developmental rate of insects in culture. *A. Rev. Ent.* **22**: 431–450.

Shaw, M.J.P. 1970*a*. Effects of population density on alienicolae of *Aphis fabae* Scop. II. The effects of crowding on the production of alatae in the laboratory. *Ann. Appl. Biol.* **65**: 191–196.

——— 1970*b*. Effects of population density on alienicolae of *Aphis fabae* Scop. II. The effects of crowding on the expression of migratory urge among alatae in the laboratory. *Ann. Appl. Biol.* **65**: 197–203.

Sokal, R.R., and F.J. Rohlf. 1981. Biometry, 2nd Ed. W.H. Freeman and Company, New York, NY. 859 pp.

Taylor, L.R. 1963. Analysis of the effect of temperature on insects in flight. *J. Anim. Ecol.* **32**: 99–117.

VanWoerkom, G.J., F.T. Turpin, and J.R. Barrett, Jr. 1980. Influence of constant and changing temperatures on locomotor activity of adult western corn rootworms (*Diabrotica virgifera*) in the laboratory. *Environ. Ent.* **9**: 32–34.

Wales, P.J., C.S. Barfield, and N.C. Leppla. 1985. Simultaneous monitoring of flight and oviposition of individual velvetbean caterpillar moths. *Physiol. Ent.* **10**: 467–472.

Weiss, M.J., K.P. Seevers, and ZB Mayo. 1985. Influence of western corn rootworm larval densities and damage on corn rootworm survival, developmental time, size and sex ratio (Coleoptera: Chrysomelidae). *J. Kansas ent. Soc.* **58**: 397–402.

Witkowski, J.F., J.C. Owens, and J.J. Tollefson. 1975. Diel activity and vertical flight distribution of adult western corn rootworm in Iowa cornfields. *J. econ. Ent.* **68**: 351–352.

Zar, J.H. 1984. Biostatistical Analysis, 2nd ed. Prentice Hall, Inc., Engelwood Cliffs, NJ.

(Date received: 30 May 1990; date accepted: 25 September 1990)